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Does selective grazing by mites and collembola affect litter fungal community structure?

M. A. McLean[1], **N. Kaneko**[2] **and D. Parkinson**[1]

[1] Department of Biological Sciences, University of Calgary, Calgary, AB, T2N 1N4 Canada
[2] Faculty of Life and Environmental Sciences, Shimane University, Matsue, Shimane 690, Japan

Summary. Effects of grazing by a common oribatid mite, *Oppiella nova*, and a common collembolan, *Onychiurus subtenuis*, alone and in combination, at field and double field densities, on the natural pine needle litter fungal community were assessed in microcosms. The animals were counted and fungi were isolated after six weeks. During the experiment, numbers of *O. nova* had doubled or quadrupled and *O. subtenuis* had reproduced in some of the microcosms. Grazing pressure by *O. nova* and *O. subtenuis*, alone or in combination, did not affect fungal species richness, diversity, dominance, or precent frequency of occurrence of 29 fungal taxa examined including taxa known to be preferred and avoided by the animals. Possible reasons for the lack of a grazing effect are discussed. Knowing the fungal food preferences of these two animals did not allow accurate predictions of the effects of grazing by these animals on the whole fungal community.

Key words: Mites, Collembola, fungal community, selective grazing, *Oppiela nova*, *Onychiurus subtenuis*

Introduction

Grazing by animals is known to affect significantly plant community structure (e.g. Brown et al. 1988; Brown & Gange 1989a; Lubchenco 1978; Paine 1966), and much speculation has been devoted to the effects of mesofauna grazing on litter and soil fungal community structure (e.g. Christensen 1989; Leonard & Anderson 1991; Moore et al. 1988; Newell 1984a, b; Parkinson et al. 1979; Visser 1985). There is ample evidence that mesofauna feed selectively and microcosm studies using a few species have shown that: i) selective grazing may alter the competitive relationships between fungi (Newell 1984b; Parkinson et al. 1979); and ii) that selective grazing may increase the rate at which primary saprophytes are replaced by secondary saprophytes (Klironomos et al. 1992). In the field there is evidence that in forest litter selective grazing alters the competitive relationship between two basidiomycete species (Newell 1984b). However, it is not known what the effects of selective grazing may be on the whole fungal community. In the present experiment the hypothesis that selective grazing by mites and collembola will affect the natural fungal community on pine needle litter was tested.

In lodgepole pine forest floor in the Kananaskis valley in SW Alberta, the most numerous species of mesofauna are an oribatid mite, *Oppiella nova* (Oudms.) and a collembolan, *Onychiurus subtenuis* Folsom (N. Kaneko, unpubl. data). Since these two species are known

Correspondence to: M. A. McLean; email malmclea@acs. ucalgary.ca

to prefer the same common litter fungi (Kaneko et al. 1996) and are the numerically dominant mesofauna in this forest floor, it is suggested that they may significantly decrease the abundance of preferred fungi in litter when they occur together. If these preferred fungal species are competitively dominant in the litter mycobiota, grazing by these animals may be expected to increase fungal species richness and diversity. Conversely, if these preferred fungi are not competitively dominant, grazing by these animals may be expected to reduce species richness and diversity. This study will also allow assessment of the relevance of laboratory feeding preference studies to faunal effects on the natural fungal community of pine litter in microcosms.

Materials and Methods

Design of Microcosms

The microcosms used were glass jars (6.5 × 5 cm dia) with screw caps and 1 cm of moistened plaster of Paris: charcoal (2 : 1) to maintain humidity. Twenty pairs of L layer pine needle litter with the naturally occurring fungal community were placed in each glass jar after determination of their moisture content.

Experimental Design

Animals were extracted from forest floor samples a few days before use, kept in similar jars at 15 °C in the dark and fed on baker's yeast until being counted and placed in the experimental chambers. To reduce the amount of fungal inoculum carried in on the animals, all the animals used in the experiment were treated with FSS (Fungizone-Streptomycin sulfate) (Moore et al. 1985) before being introduced to the experimental chambers.

Three densities of *Oppiella nova* and *Onychiurus subtenuis* were used; no animals, field densities and double field densities (0×, 1× and 2×). These densities were combined in a complete factorial design (Table 1) and each treatment was replicated three times. As well, three extra replicates without animals were set up; these were the initial controls. The experiment was conducted at 15 °C in the dark and lasted six weeks. At the end of the experiment all the adult and juvenile animals in each jar were counted.

Table 1. Mean (n = 3) numbers of *O. subtenuis* and *O. nova* added to experimental chambers and mean number of adults and juveniles recovered from experimental chambers at six weeks. Numbers of animals are 0×, 1× and 2× LF layer field densities of *c.* 3,000 m^{-2} for *O. subtenuis* and 0×, 1×, and 2× LF layer field densities of *c.* 16,500 m^{-2} for *O. nova*

O. subtenuis			*O. nova*		
Initial	Final		Initial	Final	
Adults	Adults	Juveniles	Adults	Adults	Juveniles
0	0	0	0	0	0
0	0	0	30	19	102
0	0	0	60	24	138
10	7	0	0	0	0
10	3	1	30	25	135
10	5	0	60	29	131
20	12	2	0	0	0
20	8	9	30	14	55
20	11	2	60	22	16

Fungal Community Analysis

The litter fungal community was assessed prior to (initial controls) and six weeks after the addition of the animals as percent frequency of occurrence using a washing technique (Parkinson 1994). Needles were washed, cut into 0.5 mm particles, and one particle was placed on each plate. From each replicate of each treatment, 30 particles were plated on 2% malt extract agar plus antibiotics and, in an attempt to isolate basidiomycetes, 20 particles were placed on 2% malt extract agar with antibiotics plus 5 mg L^{-1} benomyl (Worrall 1991). Fungi growing on the plates after two weeks were isolated into pure culture on malt extract agar and identified.

To assess the fungal taxa carried into the experimental chambers on the bodies of the sterilized animals, fungi were isolated from the bodies of 20 sterilized individuals of both animal species (*O. subtenuis* and *O. nova*) prior to the beginning of the experiment. One individual was placed in each petri plate containing malt extract agar and fungi growing at 2 weeks were isolated into pure culture and identified.

Statistical Analysis

Descriptive analyses of the fungal community included species abundance curves, clustering and polar ordination. Replicates within treatments were averaged for these analyses. Clustering was done using group average and % dissimilarity in Statecol (Ludwig & Reynolds 1988). Polar ordination used % dissimilarity in Statecol (Ludwig & Reynolds 1988).

The Morisita-Horn index of similarity was calculated to compare the effects of the different densities of mites and collembola on the fungal community. The effect of the treatments on the species richness, dominance and diversity of the fungal community was assessed after appropriate transformation to conform with the assumptions of ANOVA (SAS version 6.03). For simplicity, the inverse of Simpson's index was used (1/D) so that increases in the index reflect increased diversity.

Percent frequency of occurence of fungal taxa was calculated as number of particles colonized by taxon A/total number of particles per replicate (*ie.* 30) × 100. If the number of particles colonized by a particular fungal taxon was higher on the malt extract agar plus benomyl plates, the frequency of occurrence was calculated out of 20 particles. Changes in the percent frequency of occurrence of fungal taxa were assessed after appropriate transformation to conform with the assumptions of ANOVA (SAS version 6.03).

Species richness, diversity, dominance and similarity were calculated to determine if there were any significant differences between the fungal community in the initial controls and the fungal community in the six week controls.

Results

No animals were found in the control jars at the end of the experiment (Table 1). In general, there were fewer adults at the end of the experiment than were added at the beginning, but there were many juvenile *O. nova* (Table 1). Some *O. subtenuis* juveniles were produced in 2 × jars and very few in 1 × jars (Table 1).

Since fungal species abundance curves were virtually identical between treatments and polar ordination and clustering of these data did not show any pattern these analyses will not be discussed further.

There was a high degree of similarity between the fungal communities in treatments with no animals and both animals (Table 2). The fungal communities in treatments with only *O. subtenuis* or only *O. nova* were less similar to the control than to the other treatments (Table 2).

Table 2. Morisita-Horn index of similarity between fungal communities in treatments with no animals, *O. subtenuis* alone, *O. nova* alone and mixed *O. subtenuis* and *O. nova*

	O. subtenuis	*O. nova*	Both Animals
No animals	0.561	0.458	0.829
O. subtenuis	—	0.869	0.828
O. nova	—	—	0.739

Table 3. Morisita-Horn index of similarity between fungal communities in treatments with 0×, 1× and 2× field density of *O. subtenuis* and *O. nova*

	0 vs 1	0 vs 2	1 vs 2
O. subtenuis	0.778	0.821	0.917
O. nova	0.758	0.835	0.901

The fungal communities at different densities of *O. subtenuis* and *O. nova* were very similar (Table 3).

None of the measures of fungal species richness, dominance and diversity were significantly affected by *O. subtenuis* and *O. nova* either alone or in combination. Species richness and the inverse of Simpson's diversity measure are presented in Tables 4 and 5. Percent frequency of occurrence of 29 abundant fungal taxa examined was not affected by either animal at any density (Table 6). Percent frequency of occurrence of nine fungal taxa known to be preferred or avoided was not affected by either animal at either density (Table 6).

Eighteen fungal taxa were isolated from the bodies of the animals; 8 from *O. subtenuis* and 13 from *O. nova* (Table 7). These tended to be heavily sporulating genera such as *Mortierella*, *Penicillium*, *Trichoderma*, *Tolypocladium* and *Oidiodendron*. Two species were isolated from the bodies of the collembola which were not present on the needles prior to the introduction of the animals (*Penicillium* cf. *solitum* and *Chrysosporium pannorum*).

Fungal species diversity and dominance were not significantly different between the initial control and the final control (Table 8). Fungal species richness was significantly lower in the initial control than in the final control (Table 8). The Morisita-Horn index of similarity between the fungal communities in the initial and final controls was 0.562.

Table 4. Mean (n = 3) fungal species richness in treatments with 0×, 1× and 2× field densities of *O. subtenuis* and *O. nova*. There were no significant differences between any treatments ($p > 0.05$)

		Level of *O. subtenuis*		
		0	1	2
Level of *O. nova*	0	25.3	24.7	29.0
	1	25.7	25.3	26.0
	2	24.0	23.0	25.3

Table 5. Mean (n = 3) inverse Simpson diversity index for fungal communities in treatments with 0×, 1× and 2× field densities of *O. subtenuis* and *O. nova*. There were no significant differences between any treatments ($p > 0.05$)

		Level of *O. subtenuis*		
		0	1	2
Level of *O. nova*	0	12.3	15.1	20.7
	1	14.8	15.2	16.0
	2	15.8	14.0	18.1

Table 6. Mean (n = 3) percent frequency of occurrence of fungal taxa in treatments with 0×, 1× and 2× field density of *O. subtenuis* and *O. nova*. Treatments are designated as follows (mite, collembola). There were no significant differences between any treatments ($p > 0.05$). Data are presented here in condensed form, with percent frequency of occurrence of infrequently isolated taxa being summed (in each case the number of taxa summed is indicated). Analysis was performed on the original unsummed data which are available on request. * indicates taxa which were used in the fungal food preference test (Kaneko et al. 1996)

	Initial	Final							
	(0, 0)	(0, 0)	(0, 1)	(0, 2)	(1, 0)	(1, 1)	(1, 2)	(2, 0)	(2, 1)	(2, 2)
**Aureobasidium pullulans* (de Bary) Arnaud	10.0	4.4	6.7	7.8	4.4	12.2	10.0	3.3	7.8	13.3
Basidiomycetes (10 types)	7.8	28.9	17.8	18.9	18.9	31.1	14.4	6.7	1.1	8.9
*Basidiomycete 498	0.0	8.9	3.3	0.0	0.0	5.6	0.0	0.0	0.0	1.1
Chalara longipes (Pr.) Cooke	1.1	0.0	2.2	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Cladosporium 541	0.0	1.1	0.0	7.8	0.0	1.1	1.1	0.0	1.1	0.0
**Cladosporium herbarum* (Pers.) Link ex Gray	4.4	4.4	11.1	1.1	2.2	2.2	7.8	4.4	2.2	2.2
*cf. *Microstroma* 443	20.0	6.7	3.3	8.9	2.2	2.2	5.6	7.8	13.3	6.7
*cf. *Microstroma* 449	10.0	2.2	8.9	5.6	11.1	2.2	1.1	2.2	3.3	4.4
Mortierella parvispora Linnem.	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0
Mortierella ramanniana (Möller) Linnem.	0.0	1.1	0.0	5.6	2.2	0.0	5.6	7.8	5.6	3.3
Penicillium cf. *solitum* Westling	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	0.0
Penicillium lanosum Westling	0.0	0.0	1.1	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Penicillium mineoluteum Dierckx sensu Pitt	0.0	0.0	0.0	1.1	0.0	5.6	0.0	3.3	0.0	0.0
Phialophora (7 types)	1.1	1.1	4.4	2.2	0.0	6.7	4.4	7.8	3.3	2.2
Phialophora malorum (Kidd & Beaum.) McColloch	0.0	5.6	6.7	5.6	7.8	6.7	0.0	3.3	2.2	0.0
Phialophora mutabilis group	33.3	31.1	22.2	14.4	36.7	26.7	5.6	10.0	20.0	7.8
**Phoma* 445	20.0	10.0	4.4	4.4	3.3	4.4	2.2	4.4	2.2	6.7
Pycnidial forms (11 types)	20.0	17.8	18.9	21.1	18.9	14.4	22.2	33.3	5.6	25.6
Sterile dark (24 types)	16.7	23.3	10.0	31.1	33.3	36.7	40.0	37.8	46.7	47.8
*Sterile dark 516	26.7	0.0	1.1	3.3	3.3	4.4	6.7	1.1	7.8	1.1
*Sterile dark 517	10.0	7.8	17.8	8.9	16.7	6.7	18.9	8.9	7.8	15.6
Sterile hyaline (29 types)	33.3	28.9	41.1	35.6	33.3	33.3	62.2	32.2	31.1	44.4
*Sterile hyaline 487	1.1	2.2	2.2	2.2	1.1	1.1	1.1	1.1	2.2	0.0
Trichoderma atroviride Karsten	4.4	7.8	3.3	0.0	14.4	11.1	1.1	1.1	2.2	1.1
Trichoderma minutisporum Bissett	0.0	2.2	0.0	1.1	0.0	2.2	0.0	0.0	0.0	0.0
Trichoderma polysporum (Link: Fr.) Rifai	4.4	40.0	18.9	10.0	17.8	25.6	8.9	24.4	11.1	5.6
Verticillium fungicola (Preuss) Hassebrauk	2.2	0.0	0.0	3.3	0.0	0.0	0.0	2.2	0.0	0.0
Yeast-like hyphomycete	3.3	0.0	0.0	7.8	0.0	0.0	7.8	12.2	10.0	5.6
Other species (7 species)	1.1	1.1	1.1	4.4	1.1	2.2	1.1	0.0	3.3	0.0

Discussion

Much evidence exists from studies in a variety of habitats indicating that grazing can increase plant diversity through the maintenance of microsites and the reduction of dominant competitors (e.g. Brown et al. 1988; Brown & Gange 1989a; Lubchenco 1978; Paine 1966). However, plant/herbivore systems are not very good analogs for the litter fungi/mesofauna

Table 7. Mean (n = 20) percent frequency of occurrence of fungal taxa isolated from the bodies of *O. nova* and *O. subtenuis*

	O. subtenuis	*O.nova*
Trichoderma polysporum (Link: Fr.) Rifai	0.0	3.3
Trichoderma atroviride Karsten	10.0	0.0
Penicillium lanosum Westling	0.0	3.3
Penicillium 434	13.3	6.7
Penicillium cf. *solitum* Westling	20.0	3.3
cf. *Microstroma* 443	0.0	3.3
Basidiomycete 499	0.0	3.3
Mortierella ramanniana (Möller) Linnem. var. *ramanniana*	6.7	0.0
Mortierella ramanniana var. *angulispora* (Naumov) Linnem.	0.0	3.3
Mortierella humilis Linnem. ex Gams	36.7	20.0
Sterile dark 510	0.0	6.7
Cladosporium herbarum (Pers.) Link ex Gray	0.0	3.3
Alternaria alternata (Fr.) Keissler	0.0	3.3
Tolypocladium 509	10.0	0.0
Chrysosporium pannorum (Link) Hughes	3.3	0.0
Oidiodendron flavum Szilvinyi	0.0	3.3
Sterile hyaline 550	3.3	0.0
Sterile hyaline 556	0.0	6.7

Table 8. Mean (n = 3) species richness and diversity indices for the initial control (prior to start of experiment) and the final controls (end of experiment). Values within column followed by different letters are significantly different ($p > 0.05$)

Treatment	Richness	Shannon	Berger-Parker	Inverse Simpson
0 week	21.7[a]	2.71	0.203	11.9
6 week	25.3[b]	2.79	0.235	12.3

system due to spatial and temporal differences in scale and due to the inaccessibility of much of the volume of organic material to mesofauna. In a more suitable analog, the root/soil insect system, grazing by soil insect larvae decreased early successional plant species richness (Brown & Gange 1989b). The fungal community on pine needle litter is also at an early stage of succession and we might expect that grazing by mesofauna would decrease fungal species richness.

Four possible reasons why mesofaunal grazing may not affect the litter fungal community are discussed below.

i) It has been hypothesized that soil invertebrates consume only a small percentage of the fungal biomass (Mitchell & Parkinson 1976; Coleman & McGinnis 1970; Schaefer 1990). This is supported by correlational evidence from an agroecosystem which suggests that fungal biomass is primarily affected by competition, not predation (Wardle & Yeates 1993).

ii) The high variance to mean ratio typical of these fungal data reflects a highly aggregated distribution of fungi and the needles provide small scale heterogeneity, reducing the likelihood of either grazing to extinction or competitive exclusion (Armstrong 1976; Leonard & Anderson 1991). Also, fungal patchiness appears to promote compensatory fungal growth following collembolan grazing, especially in slow growing and heavily grazed fungal species (Bengtsson et al. 1993).

iii) Sectioning of pine needle litter shows that fungal mycelia are abundant below the surface (Kendrick & Burges 1962) and therefore may be inaccessible to the mesofauna.

iv) In each replicate of each treatment the fungal community (mean of 25 fungal taxa) comprised both preferred and less preferred species by both animal species under study (Kaneko et al. 1996). However, it has been shown (e.g. Klironomos et al. 1992; Mitchell & Parkinson 1976) that mites and collembola will eat and can survive and reproduce on a variety of species including those which are less preferred. Since mesofauna are known to shift from a preferred to less preferred fungal species as the preferred species is grazed down (Visser & Whittaker 1977), it is possible that, in the present experiment, the animals were shifting among different fungal species with the result that few changes in fungal percent frequency of occurrence were seen.

It is likely that all of the factors discussed above contributed to some degree to the observed lack of effect of grazing on the litter fungal community. However, given the data presented here, it is not possible to assess the relative importance of these factors. Fungal biomass changes under the different grazing regimes are being assessed and will allow clarification of the relative importance of items i and iii.

Influx of fungal inoculum on the bodies of soil fauna has been proposed by several authors as a potential means by which fungal species distributions are changed (see Visser 1985). Although two species were isolated from the bodies of the collembola which were not present on the needles prior to the introduction of the animals the importance of faunal transport of fungal propagules on the structuring of the pine needle litter fungal community cannot be assessed since there was an attempt to surface sterilize the animals. The data indicate that this sterilization was not entirely effective but compared to other studies (e.g. Christen 1975; Visser et al. 1987), relatively few fungal taxa were isolated from the animals in the present study.

During the course of the present experiment (six weeks under constant temperature and optimal moisture conditions) the needle litter decomposed from L_1 (i.e. light brown, entire) to L_2 (i.e. dark brown, entire) needles and developed a somewhat different mycobiota as shown by the fairly low similarity between the fungal communities in the initial and final controls. Some of the changes in fungal community were probably due to the growth of fungal species which were initailly present on the litter as dormant propagules. In the initial controls these species would have been washed off and therefore not isolated. To the extent that some secondary saprotrophs were already present on the litter at low abundances or as dormant propagules at the beginning of the experiment, the litter fungal community in the microcosms was probably similar to that in the field. Both in the microcosms and in the field (Tillekeratne 1989) some of the common primary saprotrophs (e.g. *Aureobasidium*, *Cladosporium*, cf. *Microstroma*, *Phoma*) become less abundant in the L_2 relative to the L_1 while some of the common secondary saprotrophs (e.g. Basidiomycetes) increase in abundance in the L_2. However, since only L material was used in the present experiment, it is not possible to be sure that under field conditions where secondary saprotrophs are abundant in lower organic layers the same result would occur. Within these limitations, the data from this experiment do not support the suggestion that selective grazing of primary saprotrophs allows colonization by secondary saprotrophs thus speeding up fungal succession as proposed by Klironomos et al. (1992).

In summary, grazing by *O. subtenuis* and *O. nova* does not appear to affect litter fungal community structure directly. The indirect effects of grazing on competition between fungi in structuring the litter fungal community are being investigated.

Although mesofaunal feeding preference tests abound, this is the first study in which a fungal food preference test has been combined with a study of the effects of grazing on the litter fungal community. Since both animals preferred the same three fungal taxa (Kaneko et al. 1996) it was expected that when both animals were present their combined grazing of the preferred taxa would decrease the percent frequency of occurrence of these taxa. Contrary to expectation, grazing by neither of the animals, alone or in combination, at any density, affected the percent frequency of occurrence of any of the preferred or avoided test fungi.

Of necessity, preference tests involve few taxa and the fungi are tested in isolation from the rest of the fungal community. In such preference tests the interactions between the fungi

are missing and these interactions may well determine the effect of grazing by mesofauna. Fungal/fungal interactions are often complex and involve the production of a variety of inhibitory and stimulatory compounds (Rayner & Webber 1984). Since mesofaunal preference for fungi depends on a variety of factors (e.g. hyphal age, hyphal activity, substrate on which the fungi were grown (e.g. Klironomos et al. 1992; Leonard 1984; Moore et al. 1987; Saichuae et al. 1972)), it is likely that compounds produced in the presence of other fungi may affect grazing patterns by mesofauna.

In summary, knowing the fungal food preferences of *O. subtenuis* and *O. nova* did not allow accurate predictions about the effects of grazing by these two animals on the litter fungal community as a whole.

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References

Armstrong, R. A. (1976) Fugitive species: Experiments with fungi and some theoretical considerations. Ecology **57**, 953–963.

Bengtsson, G., Hedlund, K., Rundgren, S. (1993) Patchiness and compensatory growth in a fungus-Collembola system. Oecologia **93**, 296–302.

Brown, V. K., Gange, A. C. (1989a) Differential effects of above- and below-ground insect herbivory during early plant succession. Oikos **54**, 67–76.

Brown, V. K., Gange, A. C. (1989b) Herbivory by soil-dwelling insects depresses plant species richness. Funct. Ecol. **3**, 667–671.

Brown, V. K., Jepson, M., Gibson, C. W. D. (1988) Insect herbivory: effects on early old field succession demonstrated by chemical exclusion methods. Oikos **52**, 293–302.

Christen, A. A. (1975) Some fungi associated with Collembola. Rev. Écol. Biol. Sol **12**, 723–728.

Christensen, M. (1989) A view of fungal ecology. Mycologia **81**, 1–19.

Coleman, D. C., McGinnis, J. T. (1970) Quantification of fungus – small arthropod food chains in the soil. Oikos **21**, 134–137.

Kaneko, N., McLean, M. A., Parkinson, D. (1996) Grazing preference of *Onychiurus subtenuis* (Collembola) and *Oppiella nová* (Acari, Oribatei) for fungal species inoculated on pine needles. Pedobiologia (in press).

Kendrick, W. B., Burges, A. (1962) Biological aspects of the decay of *Pinus sylvestris* leaf litter. Nova Hedwigia **IV**, 313–358.

Klironomos, J. N., Widden, P., Deslandes, I. (1992) Feeding preferences of the collembolan *Folsomia candida* in relation to microfungal successions on decaying litter. Soil Biol. Biochem. **24**, 685–692.

Leonard, M. A. (1984) Observations on the influence of culture conditions on the fungal preference of *Folsomia candida* (Collembola: Isotomidae). Pedobiologia **26**, 369–372.

Leonard, M. A., Anderson, J. M. (1991) Growth dynamics of Collembola (*Folsomia candida*) and a fungus (*Mucor plumbeus*) in relation to nitrogen vailability in spatially simple and complex laboratory systems. Pedobiologia **35**, 163–173.

Lubchenco, J. (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist **112**, 23–29.

Ludwig, J. A., Reynolds, J. F. (1988) Statistical Ecology: A primer on methods and computing. John Wiley & Sons, Inc., New York.

Mitchell, M. J., Parkinson, D. (1976) Fungal feeding of oribatid mites (Acari: Cryptostigmata) in an aspen woodland soil. Ecology **57**, 302–312.

Moore, J. C., Trofymow, J. A., Morley, C. R. (1985) A technique to decontaminate soil microarthropods for introduction to gnotobiotic systems. Pedobiologia **28**, 185–190.

Moore, J. C., Ingham, E. R., Coleman, D. C. (1987) Inter- and intraspecific feeding selectivity of *Folsomia candida* (Willem) (Collembola, Isotomidae) on fungi. Biol. Fert. Soil **4**, 1–7.

Moore, J. C., Walter, D. E., Hunt, H. W. (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Ann. Rev. Entomol. **33**, 419–439.
Newell, K. (1984a) Interactions between two decomposer basidiomycetes and a collembolan under sitka spruce: distribution, abundance, and selective grazing. Soil Biol. Biochem. **16**, 227–233.
Newell, K. (1984b) Interactions between two decomposer basidiomycetes and a collembolan under sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. Soil Biol. Biochem. **16**, 235–239.
Paine, R. T. (1966) Food web complexity and species diversity. Amer. Nat. **100**, 65–75.
Parkinson, D. (1994) Filamentous fungi: In: Weaver, R. W., Angle, J. S., and Bottomley, P. S. (eds) Methods of Soil Analysis, Part 2. Microbiological and Biochemical Properties. Soil Sci. Soc. Amer., Madison, WI.
Parkinson, D., Visser, S., Whittaker, J. B. (1979) Effects of collembolan grazing on fungal colonization of leaf litter. Soil Biol. Biochem. **11**, 529–535.
Rayner, A. D. M., Webber, J. F. (1984) Interspecific mycelial interactions – an overview. In: Jennings, D. H. and Rayner, A. D. M. (eds) The ecology and physiology of the fungal mycelium. Symp. of Br. Myc. Soc. Cambridge University Press, Cambridge.
Saichuae, P., Gerson, U., Henis, Y. (1972) Observations on the feeding and life history of the mite *Nothrus biciliatus* (Koch). Soil Biol. Biochem. **4**, 155–164.
Schaefer, M. (1990) The soil fauna of a beech forest on limestone: trophic structure and energy budget. Oecologia **82**, 128–136.
Tillekeratne, K. (1989) Some Aspects of the Fungal Roles in the Decomposition of Lodgepole Pine (*Pinus contorta* Loud.) and White Spruce (*Picea glauca* [Moench] Voss) Leaf Litter. Unpublished Ph.D. thesis, University of Calgary, Calgary, Canada.
Visser, S. (1985) Role of the soil invertebrates in determining the composition of soil microbial communities. In: Fitter, A. H. (ed) Ecological Interactions in Soil. Blackwell Scientific Publications, Oxford.
Visser, S., Whittaker, J. B. (1977) Feeding preferences for certain litter fungi by Onychiurus subtenuis (Collembola). Oikos **29**, 320–325.
Visser, S., Parkinson, D., Hassall, M. (1987) Fungi associated with *Onychiurus subtenuis* (Collembola) in an aspen woodland. Can. J. Bot. **65**, 635–642.
Wardle, D. A., Yeates, G. W. (1993) The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs. Oecologia **93**, 303–306.
Worrall, J. J. (1991) Media for selective isolation of hymenomycetes. Mycologia **83**, 296–302.